

Convergent evolution of two Silurian graptolites

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The two graptolite species *Cochlograptus veles* (Telychian, Upper Llandovery) and *Testograptus testis* (lower Homerian, upper Wenlock) are remarkably and uniquely similar in being strongly ventrally and planispirally coiled and in demonstrating an abrupt deflection in the immediate post-sicular regions of their rhabdosomes. The two species, however, are separated by a relatively large biostratigraphic gap and a global mass extinction, and they differ morphologically in the proportion of thecal overlap, different angles of inclination of the interthecal septa, relative proportions of the widths occupied by the free metathecae, the position of the sharp dorsal flexure relative to the tip of the sicula, and the presence of a distinctive, keel-like structure on *T. testis*. It is suggested therefore, that in spite of the strong proximal morphological parallelism between the two species, their origin is best explained as a remarkable example of convergent evolution. It is suggested that *C. veles* perhaps evolved from some modified monograptid such as *Stimulograptus*, whereas the small *Testograptus* group may have derived from some monograptid such as *Monograptus flemingii*. Cladistic analysis fully supports the independent derivation of the two species. If correct, this hypothesis supports the validity of separate generic names for the two species, despite the close and unique rhabdosomal similarities, including proximal metathecal form.

Key words: Graptoloidea, Monograptidae, taxonomic nomenclature, convergent evolution, pseudovirgula, Llandovery, Wenlock.

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Introduction

The species *Cochlograptus veles* (Richter, 1871), and its synonym *Monograptus discus* Törnquist, 1892 has been known for more than 100 years, but most of the limited understanding of its morphology has been based on flattened and sometimes tectonically deformed specimens. The species was assigned by Obut (1987) to *Cochlograptus*, but that material, being based on only moderately preserved, flattened specimens, adds little to the greater understanding of its morphology. The discovery by Loydell and Cave (1994) of post-sicular development by means of a pseudovirgula and the illustration of several very well preserved, isolated specimens of the species by Maletz (2001), two of them having pseudovirgular development, show the species to be very unusual, and worthy of further detailed study. The recovery of numerous isolated, un-compressed, immature specimens from limestone concretions from three separate localities in the Arctic Islands, Canada, adds much to the understanding of its morphology, and morphological and developmental variation. Most strikingly, the species is remarkably similar in many characteristics to the larger and much younger *Testograptus testis* (Barrande, 1850), in its strong planispiral ventral curvature of the rhabdosome, general thecal morphology and, particularly, in the sicular and immediately post-sicular regions, including the rare occurrences of development by means of a pseudovirgula. The present study: (i) details the morphology of *C. veles*, and

compares it with that of *T. testis*, with particular focus on their proximal regions, showing them to be mutually unique and remarkably similar species; (ii) looks into the possible origins of the two morphologically uniquely similar, but biostratigraphically widely-separated species, asking whether they represent a single lineage or were products of convergent evolution; (iii) discusses the nomenclatural implications.

Institutional abbreviations.—BGR, Bundesanstalt für Geowissenschaften und Rohstoffe, Berlin; GSC, Geological Survey of Canada, Ottawa; ROM, Royal Ontario Museum, Toronto.

Biostratigraphy of study material

The Arctic co-occurrence of *Cochlograptus veles*, *Monograptus marri*, *Oktavites spiralis*, and *Oktavites cf. falx* from the Cape Sir John Franklin, Devon Island, Canadian Arctic Archipelago, suggests an age within the generalized upper Telychian, *Oktavites spiralis* Biozone (sensu the biozonal scheme of Koren' et al. 1995). A small number of specimens of *C. veles* from Cape Manning, northeastern Cornwallis Island co-occur with *Streptograptus exiguus*, *Torquigraptus* sp., and *Spirograptus turriculatus*, pointing to a correlation with the *Spirograptus turriculatus*–*Monograptus crispus* Biozone of Koren' et al. (1995), whereas its association with *Monograptus priodon*, *Stomatograptus* sp., *Monoclimacis*

ex. gr. *griestoniensis*, and *Monoclimacis* ex gr. *vomerina* from Cape Phillips, Cornwallis Island, suggests a correlation with the *Monoclimacis griestoniensis*–*Monoclimacis crenulata* Biozone of Koren, et. al. (1995). The suggested ages are well within the range of those of *Cochlograptus veles* observed elsewhere: the *Monograptus crispus* Biozone and higher in the British Isles (Rickards 1976; Loydell and Cave 1994); *Monograptus crispus* through lower *Oktavites spiralis* biozones in the Czech Republic (Štorch 1994); *Spirograptus turriculatus* to *Monoclimacis griestoniensis* biozones in Scandinavia (Törnquist 1892; Bjerreskov 1975; Maletz 2001); *Spirograptus turriculatus* Biozone in Poland (Tomczyk et al. 1990); *Spirograptus turriculatus* to *Monoclimacis griestoniensis* biozones in Taimyr and Siberia, Russia (Obut et al. 1965; Obut and Sobolevskaya 1975; Obut, 1987); *Spirograptus turriculatus* to *Oktavites spiralis* biozones in Germany (Hundt 1965; Schauer 1971) and *Spirograptus turriculatus* Biozone in the Mackenzie Mountains, north-western Canada (Lenz 1988).

Testograptus testis is a well-known and widespread “index” for the lower Homerian (upper Wenlock) *Cyrtograptus lundgreni*–*Testograptus testis* Biozone of Lenz and Melchin (1991) or, simply, the *Cyrtograptus lundgreni* Biozone of Lenz and Kozłowska-Dawidziuk (2001). The time-interval between the ranges of the two species involves 6–7 Ma (Melchin et al. 2004).

Systematic paleontology

Order Graptoloidea Lapworth, 1873

Family Monograptidae Lapworth, 1873

Genus *Cochlograptus* Obut, 1987

Type species. Nautilus veles Richter, 1871, Upper Llandovery, Thuringia, Germany. Lectotype BGR X 1154a from original Richter collection chosen by Maletz (2001: fig. 3A).

Emended diagnosis.—Disk-shaped, ventrally and continuously planispiral rhabdosome, possessing 1.5–2 whorls. Thecae of monograptid type, hook-shaped, curved with drawn-out ends and strongly inflated, with well-developed lateral spines. Sicala moderately to strongly ventrally curved. Prominent triangular rutellum on sicala. Rhabdosome sharply ventrally deflected near tip of sicala. Post-sicular development via strongly deflected nema or, rarely, pseudovirgula that originates slightly below tip of sicala.

Cochlograptus veles (Richter, 1871)

Figs. 1A–H, 2A, B, 4C–F, 5B.

1871 *Nautilus veles* Richter: 243, text-fig. 1.

1883 *Monograptus discus* sp. nov.; Törnquist 1883: 24.

1892 *Monograptus discus* Törnquist; Törnquist 1892: 39, pl. 3: 27, 28.

1913 *Monograptus discus* Törnquist; Elles and Wood 1913: 439, pl. 44: 5a–d; figs 302a–c.

1965 *Monograptus veles* (Richter); Obut et al. 1956: 52, pl. 7: 2–4.

1965 *Monograptus veles* Richter; Hundt 1965: figs. 93, 137, 200.

1970 *Monograptus discus* Törnquist; Rickards 1970: 76, pl. 6: 8.

1971 *Monograptus* (*Monograptus*) *veles* (Richter); Schauer 1971: 59, fig. 5; pl. 35: 1–3; pl. 36: 16–18.

1975 *Monograptus veles* (Richter); Bjerreskov 1975: 71, pl. 11: D.

1975 *Monograptus veles* (Richter); Obut and Sokolevskaya 1975: 168, pl. 33: 3, 4.

1987 *Cochlograptus veles* (Richter); Obut 1987: 142, pl. 25: 5–10.

?1987 *Cochlograptus chaletzkae* Obut 1987: 143, pl. 25: 11, 12.

1988 *Monograptus veles* (Richter); Lenz 1988: 1963, fig. 5P–S.

?1993 *Monograptus veles* (Richter); Štorch and Serpagli 1993: 40, fig. 12C, E; pl. 7: 5, 7.

1994 *Cochlograptus veles* (Richter); Loydell and Cave 1994: 611, figs. 1.1–1.3, 2.

1994 *Monograptus veles* (Richter); Štorch 1994: fig. 6K.

2001 *Cochlograptus veles* (Richter); Maletz 2001: 172, fig. 3A–I.

Material examined.—About 40 specimens from talus nodule 2A, and one to three specimens from each of talus nodules 2C, 4B, and 110T, all from the Cape Sir John Franklin (76°42.5'N, 96°53'W), westernmost Devon Island (SJF 02); two specimens each from Cape Manning section 3, collections CM3, 6.1 m and 10.2 m (75°26.8'N, 94°16.7'), Cornwallis Island; and eight specimens from the Cape Phillips type section, collection CP98, 6.4 m (75°37.3'N, 94°31'W), Cornwallis Island. All specimens isolated and uncompressed, and all immature.

Description.—Rhabdosome tightly, ventrally, and planispirally coiled; most mature isolated study specimen with five complete thecae (Fig. 4C) and prothecal part of theca 6, coiled through about 270°. Sicala total length 0.8–0.9 mm and about 0.14 mm across aperture; prosicula is 0.34–0.35 mm long. Sicala aperture with narrow, well-developed rutellum, virgella about 0.4 mm long. Junction of prosicula and metasicala rarely marked internally by annulus (see Lenz and Kozłowska-Dawidziuk 1998). Porus distal rim positioned 0.04–0.06 mm distal of sicala aperture. Sicala moderately to strongly ventrally curved, the greatest curvature being in the distal half of metasicala; tip of prosicula straight to curved ventrally. Tip of prosicula seldom fully preserved and where fully preserved may be composed only of longitudinal threads, particularly on dorsal side (Fig. 1A), and proximalmost tip may often be abruptly flexed ventrally. Nema often arises asymmetrically from tip of sicala or, less frequently, from the ventral side slightly below the tip, in which case the extreme tip of sicala is distally projected as a small, mound-like protuberance (Fig. 1B₂, E, G). In rare specimens, a pseudovirgula emerges from a point below the tip of the prosicula (Fig. 4F₁–F₃) and replaces the nema as the growth axis along the dorsal side of the rhabdosome. In either case, nema or pseudovirgula is sharply deflected ventrally at angle of 45–60° to longitudinal axis of sicala (Fig. 1B, F, H; see also Maletz 2001: fig. 3G, H). Apex of sicala attains level from midway between thecae 1 and 2 to, most commonly, about level with thecal hood of theca 2. Thecae multiform. Theca 1 arises 0.04–0.06 mm from sicular aperture; metatheca relatively long and strongly curved through about 180° so that aperture fully directed proximally. Theca 2 metatheca somewhat less strongly curved than theca 1, aperture directed slightly proximo-ventrally. Theca 3, arising after the strong ventral deflection of the nema or pseudovirgula, typically possesses an unusually long protheca to

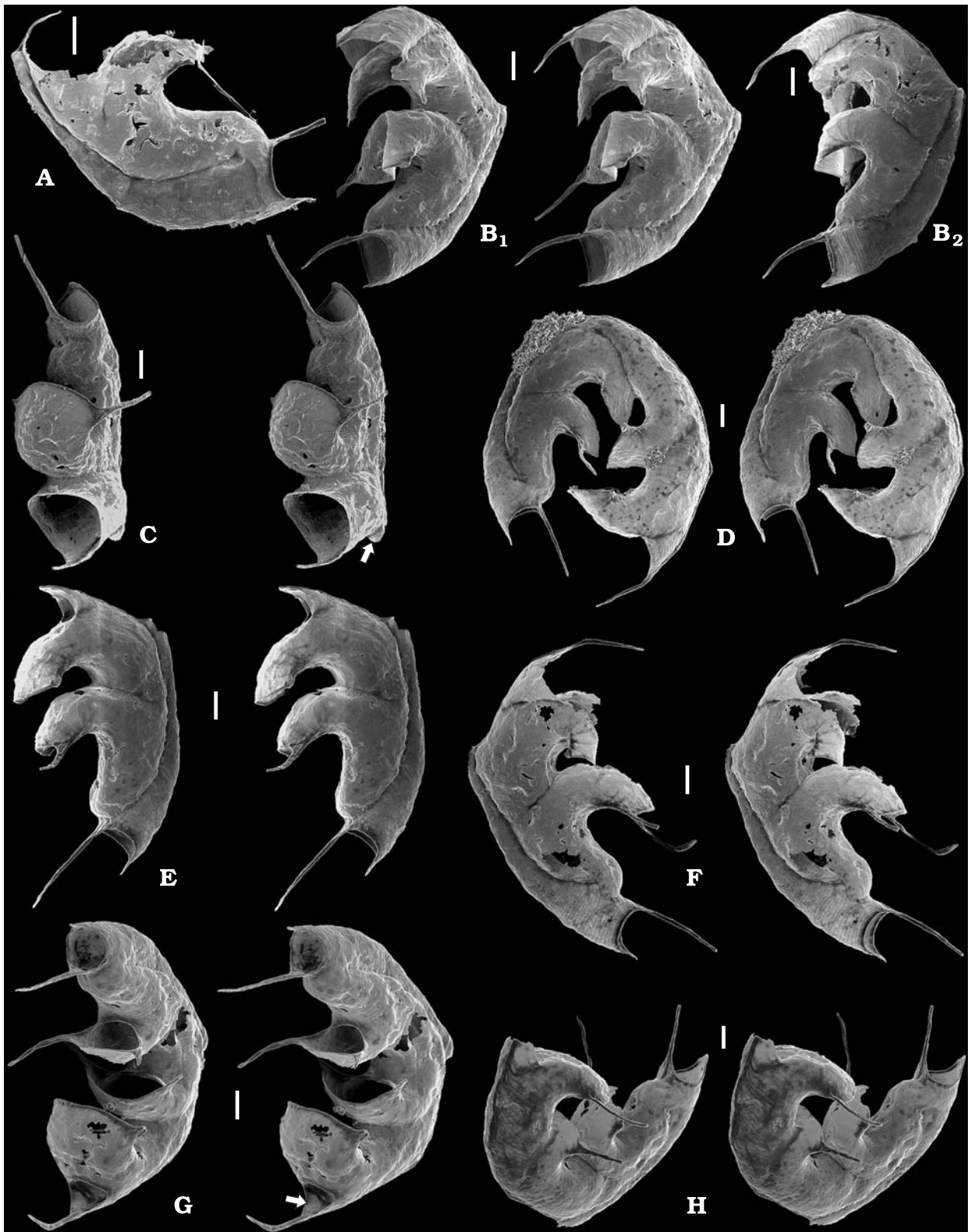


Fig. 1. Silurian graptolite *Cochlograptus veles* (Richter, 1871). All collections from SJF-02, nodule 2A. **A.** Full profile of specimen showing theca 1 arising out of sicula very close to aperture and strong ventral flexures of nema and sicular threads, GSC34900. **B.** Full profile and slightly oblique view of specimen GSC 34901; **B₁**, stereopair; **B₂**, full profile. **C.** Stereopair, ventro-lateral view of specimen with complete theca 1 and protheca of theca 2, and showing free tip of sicula (arrow), GSC 34902. **D.** Specimen with four complete thecae and protheca of theca 5, GSC34903. **E.** Stereopair showing two fully developed thecae and protheca of theca 3; note well-developed rutellum, GSC34904. **F.** Full profile stereopair showing abrupt flexure of nema away from tip of sicula, GSC34905. **G.** Oblique view stereopair showing three fully developed thecae and the common canal leading to theca 4 (arrow), GSC34906. **H.** Stereopair distal view of fully developed thecae and protheca of theca 4, and well-developed rutellum and protuberance of sicula tip, GSC34907. Scale bars 100 μ m.

compensate for strong and abrupt flexure. More distal thecae with smoothly and uniformly curved dorsal walls, with relatively short, triangular prothecae and long, strongly curved metathecae in which the apertures of thecae directed ventroproximally, and lateral profiles of distal metathecae are triangular. Amount of curvature and thecal overlap gradually decreases distally. Thecal apertures ovate in cross section, apertural rim smoothly curved with slightly thickened margin. Thecal spines about 0.3–0.4 mm long at lateral margin of apertural hood, directed laterally or slightly ventro-laterally. Thickened interthecal septum (see Lenz and Kozłowska-Dawidziuk 1998) well developed (Fig. 2A₄, B₂). Interthecal septum curved, angle of its junction with dorsal wall of rhabdosome is somewhat variable but approximately 60° throughout the length of the rhabdosome. Thecal overlap 25–30% of total thecal length, decreasing somewhat distally. Proportion of rhabdosomal width occupied by free metathecal portions about 50% throughout. 2TRD approximately 1 mm from second to fourth thecae; width at theca 1 about 0.5 mm, and 0.6 mm at theca 5 (one specimen).

Remarks.—Although Obut (1987) assigned this species to the subgenus *Cochlograptus*, Loydell and Cave (1994) and Maletz (2001) accorded it full generic status, a practice followed in this paper. *Cochlograptus veles* (and its junior synonym “*Monograptus*” *discus*), has been recorded from many regions in the world: Germany (Richter 1871; Hundt 1965; Schauer 1968; Maletz 2001), Scandinavia (Törnquist 1892; Bjerreskov 1975; Maletz 2001), British Isles (Elles and Wood 1913; Rickards 1970; Hutt 1975; Loydell and Cave 1994), southern Mackenzie Mountains, Canada (Lenz 1988), Canadian Arctic Islands (Melchin 1989), Taimyr, Russia; Central Asia (Obut et al. 1965; Obut and Sobolevskaya 1975; Obut 1987), Czech Republic (Štorch 1994), Poland (Tomczyk et al. 1990) and, questionably, Sardinia (Štorch and Serpagli 1993), from which the specimens show a much looser ventral curvature. All of the specimens, except for the three isolated specimens from Sweden illustrated by Maletz (2001), have been either preserved as flattened films on shale surfaces or, occasionally, shown in slight relief. In either case, details of the sicula, thecae, and early rhabdosomal development have been poorly understood. This is especially true in the case of mature flattened material, where more extended development of the rhabdosome completely obscures details of the early proximal development.

The genus *Cochlograptus* was erected by Obut (1987), who considered the tightly coiled, discoid nature of the rhabdosome to be the definitive generic character. He recognized the *Monograptus priodon*-like shape of the thecae with their pronounced, laterally projecting spines, and noted the similarity of the new genus to *Testograptus testis* from which it is distinguished in being totally discoid-shaped, and in being much smaller. However, in all earlier studies of flattened specimens of the species, including those studied by Obut (1987), there was little to indicate that the dorsal wall margin was other than a smoothly rounded spiral throughout or, if observed, this was ignored or unappreciated. This lack of appreciation was most probably due to the fact that all previ-

ously studied and illustrated forms were flattened and more mature, in which case, early rhabdosome growth was obscured by later development.

Loydell and Cave’s (1994) study of several immature specimens of *Cochlograptus veles* was the first to illustrate its unusual development, wherein the nema and the tip of the prosicula are free, and a pseudovirgula, appearing and diverging strongly from a point near the tip of the sicula, performs the same post-sicular functions as the true nema for all remaining thecae subsequent to the formation of thecae 1 and 2. Maletz (2001) illustrated some specimens from Richter’s (1871) original material, selected a lectotype from another slab collected by Richter and, importantly, illustrated three immature, isolated specimens from Sweden. Two of these specimens (e.g., Maletz 2001: fig. 3G, H) clearly show the free tip of the sicula and nema, although much less of the sicular tip is exposed than for the specimen illustrated by Loydell and Cave (1994). This may, however, be the result of continued growth of the triangular web of material in the early growth stage shown in Loydell and Cave (1994: fig. 1.3). These specimens also demonstrate the sharp angle between the pseudovirgula and the sicula-nema axis.

The Arctic collections, while numerous, are made up of entirely immature specimens, with no specimen possessing more than five fully-developed thecae and the protheca of theca 6. The fact that *Cochlograptus veles* (as well as *Testograptus testis*) develop with a “normal” nema as well as, occasionally, by means of pseudovirgula, suggests that both modes of growth are part of the normal range of variation within these two species. It demonstrates, moreover, the “plasticity” and the adaptability of graptolites in their overall astogenetic development.

Rickards, Hutt and Berry (1977) suggested that “*Monograptus discus*” (= *Cochlograptus veles*) may have been commonly helically spiralled. The many isolated specimens from the Arctic, the isolated Swedish specimens with at least six fully-developed thecae (Maletz 2001), the well-preserved, and much more mature specimen (with more than 20 thecae) illustrated by Bjerreskov (1975), and the dozens of flattened specimens illustrated in Hundt (1965) suggest, however, that *C. veles* was totally planispiral. Alternately, if the species was helically spired, the spire would have been exceedingly shallow.

Genus *Testograptus* Příbyl, 1967

Type species: *Graptolithus testis* (Barrande, 1850), Upper Wenlock, Barrandian region, Czech Republic.

Emended diagnosis.—Rhabdosome planispirally and ventrally coiled; proximal end much more strongly curved than distal; total curvature ranging 270–450°. Rhabdosomal development occasionally by means of pseudovirgula. Thecae biform, hooked, with long, paired, laterally directed spines. Proximal-most thecae with strongly hooked metatheca, distal thecae with lesser hook. Thecal overlap about 50–75%. Sicula weakly and ventrally curved. Distal of sicular apex, rhabdosome abruptly ventrally flexed through 30° to greater

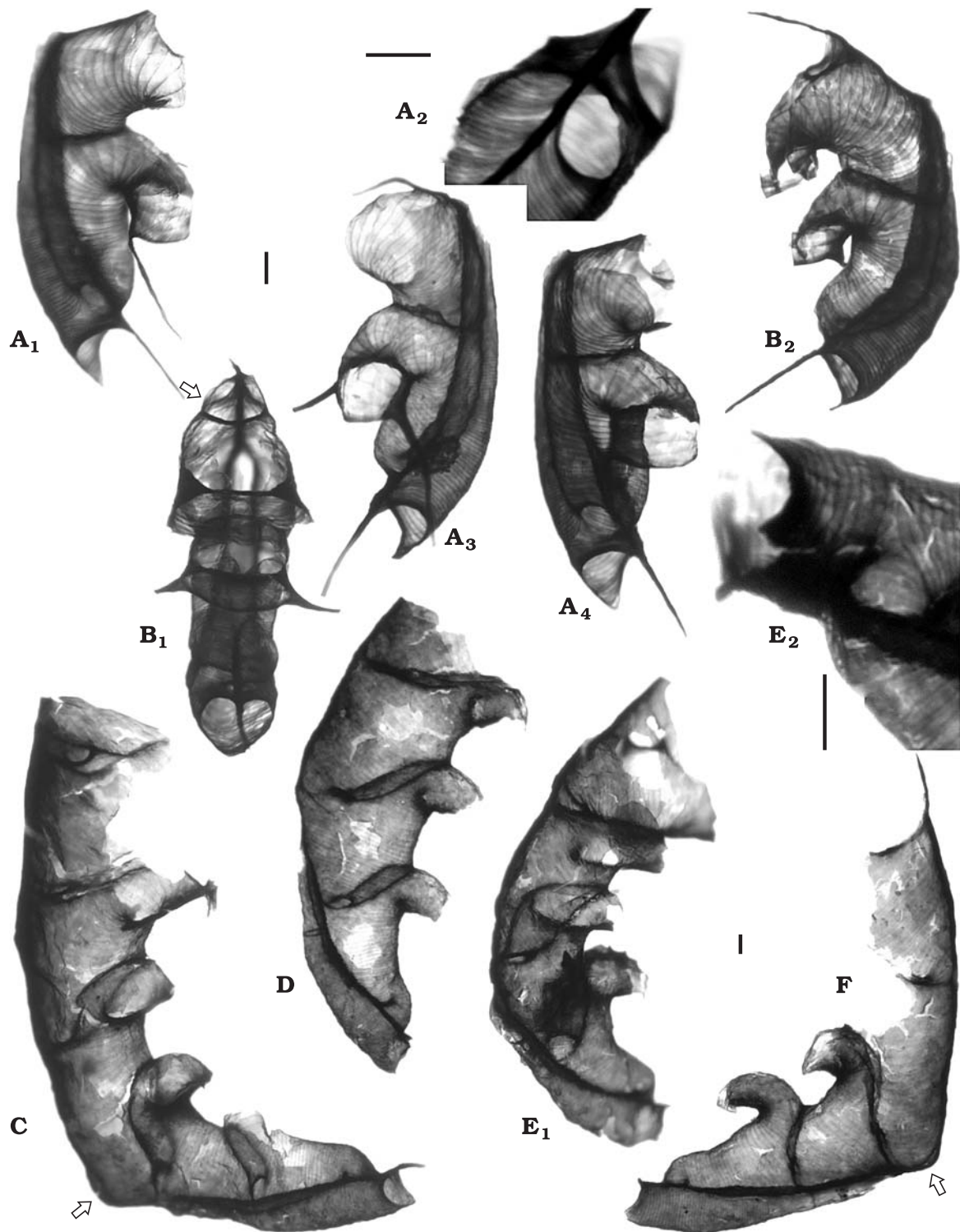


Fig. 2. Silurian graptolites *Cochlograptus veles* (Richter, 1871) (A, B) and *Testograptus testis* (Barrande, 1850) (C–F) in direct comparison. Chemically cleared and infrared views of specimens from collection SJF-02, talus nodule 2A, Cape Sir John Franklin, Devon Island. A. Various oriented views of specimens with two developed thecae and common canal of theca 3, GSC34908; A₁, profile view; A₂, enlargement showing normal porus; A₃, dorso-lateral view; A₄, ventro-lateral view. B. Ventral and lateral views of specimen, GSC34909; B₁, ventral view showing tip of sicula (clear region) and well marked thickened intertheatal septum (arrow); B₂, profile showing well-developed nema. (C–F) *Testograptus testis* (Barrande, 1850). Chemically cleared and infrared images of specimens from collection RC01-2, 2.5 m, Rookery Creek, Cornwallis Island. C. Largest specimen profile showing deflexed nema distal of sicula tip, and hollow, keel-like protuberance distal of sicula tip (arrow), GSC34910. D. Profile of specimen with only gentle ventral flexure and moderately curved sicula, GSC34911. E. Near-profile view of specimen and enlargement of distal end of sicular region, GSC34913; E₁, profile view of cleared specimen; E₂, enlargement showing normal porus. F. Specimen with well-preserved two proximal thecae, strong ventral flexure, and hollow protuberance (arrow) distal of tip of sicula, GSC34913. Scale bars 100 μ m.

than 90°. Point of flexure often developed into sharp, keel-like prominence, which is apparently hollow.

Species included.—*Testograptus testis* (Barrande, 1850) and *Testograptus cubitus* Lenz and Kozłowska, 2006.

Testograptus testis (Barrande, 1850)

Figs. 2C–F, 3A–F, 4A, B, 5C.

1850 *Graptolithus testis* sp. nov.; Barrande 1850: 52, pl. 3: 19–21.

Abridged synonymy follows:

1913 *Monograptus testis inornatus* Elles; Elles and Wood 1913: 446, pl. 44: 7a, b; text-fig. 307a, b.

1974 *Monograptus (Testograptus) testis* (Barrande); Urbanek and Teller 1974: 237, text-figs. 1–5; pl. 22: 1–3; pl. 23: 1, 2; pl. 24: 1.

1990 *Monograptus testis* (Barrande); Lenz 1990: 177, fig. 1: 1–12; fig. 2: 1–10.

1991 *Monograptus testis testis* (Barrande); Lenz and Melchin 1991: 231, fig. 8a–c.

1991 *Monograptus testis incomptus* ssp. nov.; Lenz and Melchin 1991: 231, figs. 7a, b, 17D, E, I, J.

1999 *Testograptus testis* (Barrande); Kozłowska-Dawidziuk 1999: 355, fig. 2C.

2001 *Testograptus testis incomptus* Lenz and Melchin; Lenz and Kozłowska-Dawidziuk 2001: 11, pl. 3: 1, 10, 15.

2006 *Testograptus testis* (Barrande); Lenz and Kozłowska 2006: figs. 13.1, 13.4, 13.7.

Material.—More than 30 immature, isolated specimens from the *Cyrtograptus lundgreni* Biozone, upper Wenlock, of Rookery Creek (RC01-2; 75°22.5'N, 95°41'W), and several from Snowblind Creek (SB-E; 75°11.6'N, 93°51'W), north-eastern Cornwallis Island, two of which show a well-developed pseudovirgular growth mode. Associated with *Cyrtograptus lundgreni* Tullberg, 1883, the index species for this biozone, the very common retiolitid *Eisenackograptus eisenacki* Kozłowska-Dawidziuk, 1990, and *Cyrtograptus hamatus* (Bailly, 1861), *C. radians* Törnquist, 1887, and *Testograptus cubitus* Lenz and Kozłowska, 2006, the last three taxa restricted to the *Cyrtograptus lundgreni* Biozone.

Remarks.—For this paper, and following Loydell and Cave (1994) and Lenz and Kozłowska-Dawidziuk (2001), the name “*Testograptus*” is used in the full generic sense, rather than as a subgenus as originally proposed by Přibyl (1967). This species has been earlier described by Urbanek and Teller (1974) and Lenz (1990), both studies being based on isolated, undeformed specimens. Beyond the details in these descriptions, further important morphological features include the abrupt ventral deflection in the post-sicular region of the rhabdosome (already noted by Urbanek and Teller 1974), a positioning of the proximal rim of the porus 0.06–0.08 mm proximal of the sicula aperture (Fig. 2E₂), and the very rare occurrence of development by means of a pseudovirgula (Fig. 4A, B), the last feature paralleling that seen in rare specimens of *Cochlograptus veles*. Additional features include thecal overlap ranging from about 50% proximally to about 75% distally, and proportion of rhabdosomal width occupied by free metathecal portions consistently about 25–30%. In addition, the angle formed between the interthecal septum and the dorsal wall of the rhabdosome decreases from 70–80° to only 40–50° dis-

tally, as the degree of thecal overlap increases. Relevant comparative morphological details for *Testograptus testis* and *Cochlograptus veles* are detailed in the next section. 2TRD from second to fourth thecae 1.1–1.4 mm; width at theca 1 about 0.7 mm, and 0.8 mm at theca 5.

The range of variation in proximal rhabdosomal curvature seen in the present collections suggests that the supposedly distinct subspecies *T. testis testis*, *T. testis incomptus*, and *T. testis inornatus* may be part of a single, variable population, rather than being separate subspecies, as earlier accepted by Lenz and Melchin (1991).

A recently described species of *Testograptus*, *T. cubitus* Lenz and Kozłowska, 2006, from the *Cyrtograptus lundgreni* Biozone of Arctic Canada (Lenz and Kozłowska 2006), but distinctly differing from *T. testis*, also demonstrates the abrupt post-sicular ventral deflection with a prominent, keel-like protuberance, exactly as seen in the typical form.

Morphological comparison

Testograptus testis and *Cochlograptus veles* are among the very few pre-Ludlow species of graptolites that demonstrate strong planispiral, ventral coiling. *Pseudostreptograptus williamsi* Loydell, 1991 (text-fig. 19.1–7) and *Streptograptus sinicus* Ge, 1974 (see Chen 1984: pl. 17: 7, 8, 12–14), both Llandovery species, also demonstrate strong ventral coiling, but the thecae in both are totally different. The most striking shared features of the two species under discussion are the very similar sicular and proximal thecal forms and, above all, the very abrupt and strong ventral deflection of the rhabdosome at, slightly proximal to, or slightly distal of, the tip of the sicula. The sharp deflection occurs at or near the base of the third theca, a feature that was well illustrated in the Urbanek and Teller (1974) study of *T. testis* in which they noted the “angular bending”. The deflection in *T. testis*, however, consistently occurs about 0.2–0.3 mm distal of the sicular tip (Fig. 3B, D₂, E, F₁), whereas that in *Cochlograptus veles* is more or less at, or asymmetrically disposed at or near the tip of the sicula (Fig. 1B₂, C, E, F). Further, the resulting “angular bending” is generally abrupt (sometimes greater than 90°), and often develops into a distinctive, sharp, keel-like, and apparently hollow, protuberance on *T. testis* noted above (Figs. 2C, F [arrows], 3B, D₂, E, F). This structure has never been seen in *C. veles*. In the rare case of development through a pseudovirgula, the emergence of the pseudovirgula and the deflection in *T. testis*, as in *C. veles*, originates slightly below the tip of the sicula (Fig. 4A, B). Normally, the sharp flexure in *C. veles* occurs about mid-length of theca 2, whereas in *T. testis* the abrupt flexure most commonly occurs distally in about the proximal one-third of the protheca of theca 3 (see Fig. 3D₂). This feature is also readily seen in *T. testis* as illustrated by Urbanek and Teller (1974: text-figs. 1, 2) and Lenz (1990: figs. 1.1, 1.2, 1.4, 1.5, 1.8, 1.11, and 2.9), and in *Testograptus cubitus* Lenz and Kozłowska, 2006 (figs. 13.5, 13.6, 13.8–13.14).

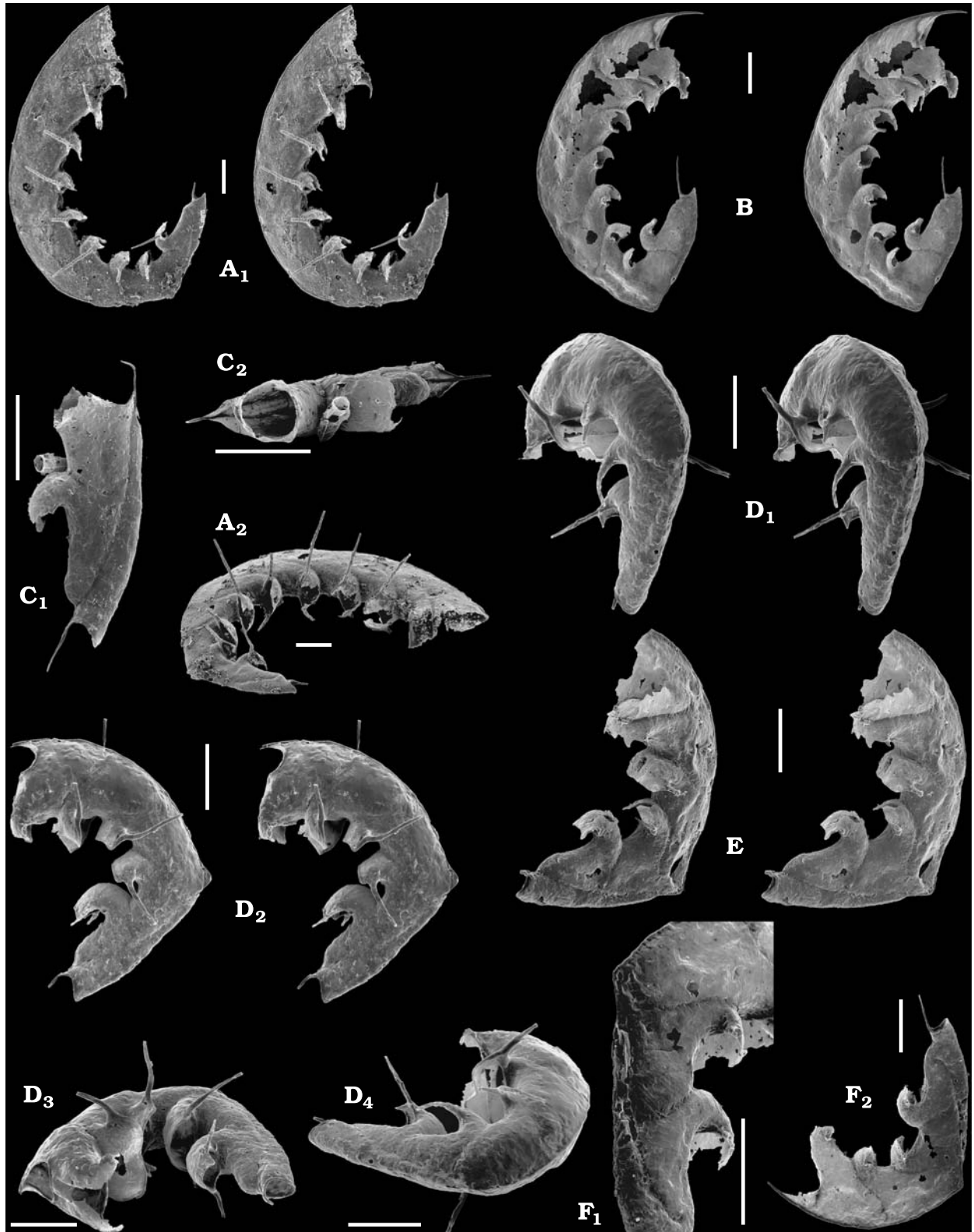


Fig. 3. Silurian graptolite *Testograptus testis* (Barrande, 1850). All collections from section RC01-2, 2.5 m, Rookery Creek, Cornwallis Island. **A.** Largest specimen, stereopair profile and ventro-lateral view, GSC34914; **A**₁, profile view; **A**₂, ventro-lateral view showing long, laterally projecting thecal spines. **B.** Stereopair of specimen with very strong dorsal flexure and prominent keel-like protuberance at point of flexure, GSC34915. **C.** Lateral and ventro-distal view of specimen, GSC34916; **C**₁, with strongly dorsally flexed nema; **C**₂, nema strongly ventrally flexed. **D.** Various views of specimen GSC34917; **D**₁, dorso-lateral view stereopair; **D**₂, ventro-lateral view stereopair showing prominent keel-like protuberance at point of flexure; **D**₃, ventral view; **D**₄, dorso-lateral view, V-shaped protuberance at point of flexure. **E.** Stereopair of specimen with strong ventral flexure and prominent protuberance distal of sicular tip, GSC34918. **F.** Dorso-lateral and lateral views of specimen, GSC34919; **F**₁, dorso-lateral view showing prominent flexure; **F**₂, profile view. Scale bars 500 μ m.

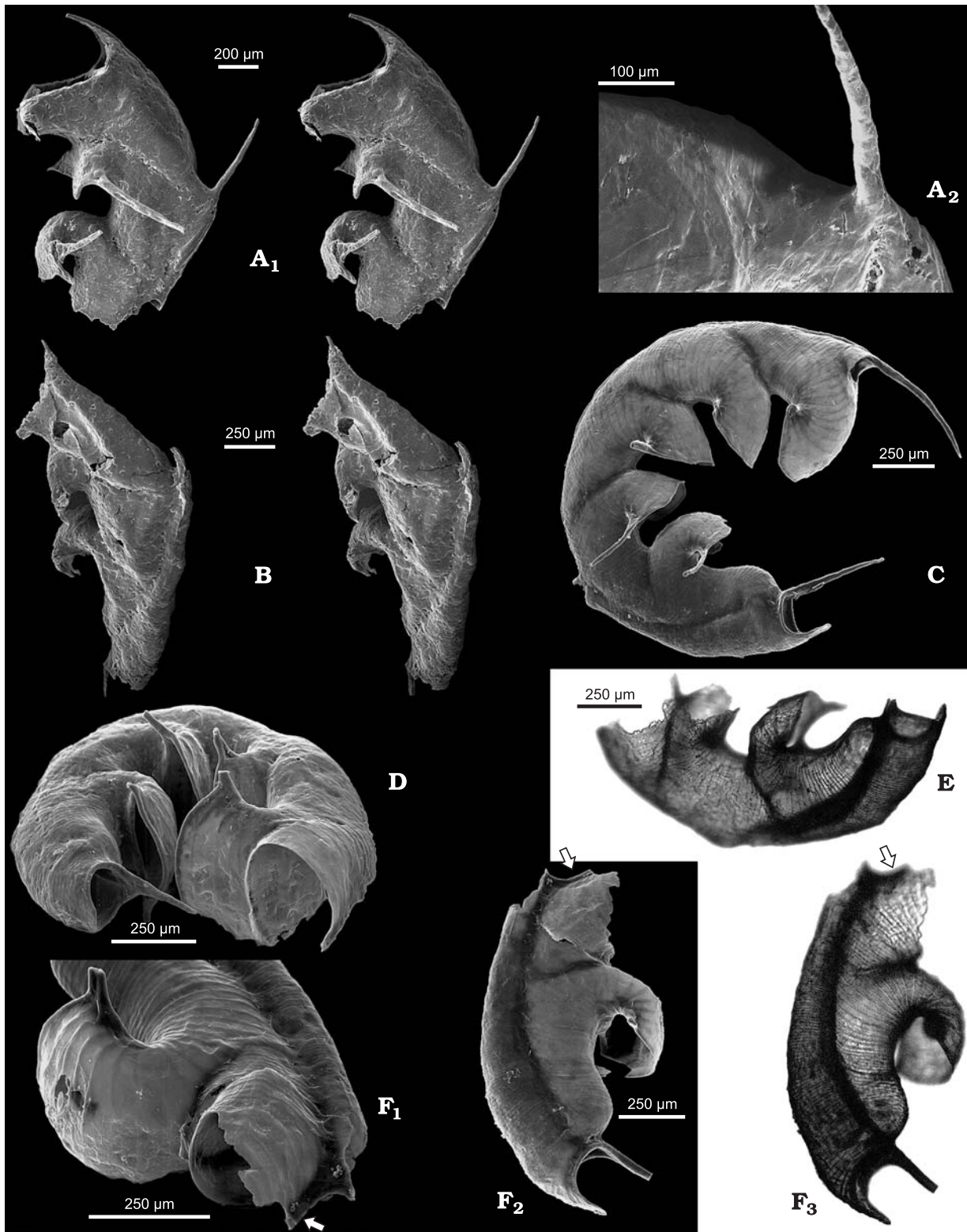


Fig. 4. Silurian graptolites *Testograptus testis* (Barrande, 1850) (A, B) and *Cochlograptus veles* (Richter, 1871) (C–F) in direct comparison. Specimens from SB-E, 49 m, Snowblind Creek, Cornwallis Island. A. Fragment of specimen with pseudovirgula development, GSC34920; A₁, stereopair showing isolated nema; A₂, enlargement to show nema area, and infilling between pseudovirgula and nema. B. Stereopair of dorso-lateral view of specimen with free nema and subsequent development of rhabdosome via a pseudovirgula, GSC34921. (C–F) *Cochlograptus veles* (Richter, 1871); from CP98, 6.4 m, Cape Phillips, Cornwallis Island (C, F) and from CM3, 6.1 m, Cape Manning Cornwallis Island (D, E). C. Extremely well-preserved specimen, showing blunt-ended sicula and flexure; note well-developed rutellum, GSC34922. D. Ventro-lateral view of well-preserved specimen showing four complete thecae, GSC34923. E. Infrared image showing strongly curved sicula, GSC34924. F. Views of a specimen showing a pseudovirgula (arrows) and exceptionally long rutellum, GSC34925; F₁, distal view enlargement; F₂, SEM image; F₃, infrared image.

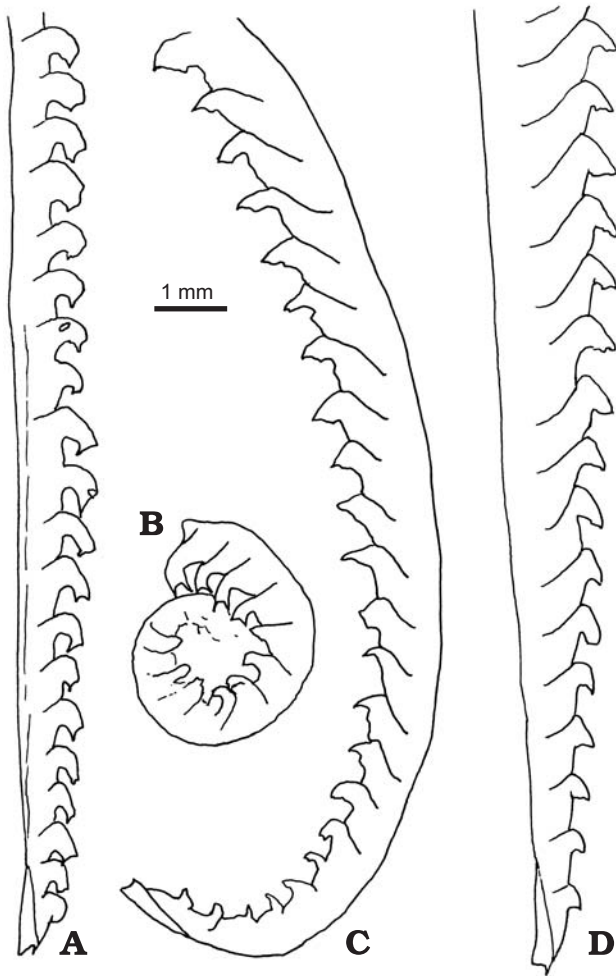


Fig. 5. Line drawings of four monograptid species to compare thecal characteristics. **A.** *Monograptus?* cf. *ayagusensis* (Obut and Sobolevskaya, 1966) compressed mature specimen from Twilight Creek (TC), Bathurst Island, TC 27.5 m (Melchin 1989) showing thecae very similar to those seen in *Cochlograptus veles*, GSC34926. **B.** *Cochlograptus veles* (Richter, 1871), compressed mature specimen from Twilight Creek, Bathurst Island, TC 27 m (Melchin 1989), ROM46027. **C.** *Testograptus testis incomptus* (Lenz and Melchin, 1991) holotype, compressed specimen from Rookery Creek (RC), Cornwallis Island, RC 284 m (Lenz and Melchin 1991: figs. 7B, 17I), GSC95423. **D.** *Monograptus flemingii* (Salter, 1852), compressed specimen from Prairie Creek (PC), Northwest Territories, PC 210 m (Lenz 1988: pl. 1: A), GSC91494.

Other differences between the two species reside in the sicular aperture characteristics, rhabdosomal shape, proportion of overlap of thecae (about 25–30% in *C. veles*, about 50–75% in *T. testis*), profile and shape of, particularly, distal thecae (more isolated and more triangular in distal theca of *C. veles*), and the proportion of the relative width of the rhabdosomal width occupied by the free portion of the metathecae (at least 50% in *C. veles* compared with only about 25% in *T. testis*). The sicular aperture of *C. veles* possesses a prominent v-shaped rutellum, whereas that of *Testograptus testis* lacks such a structure. *Testograptus testis* has a looser coil sometimes resembling the number six, although the degree of coiling varies considerably, whereas *C. veles* is a tightly coiled disk throughout. *T. testis* rhabdosome dimen-

sions and sicular length are about double of those of *C. veles*. Further distinctions include the abrupt deflection slightly below or at the tip of the sicula in *C. veles* compared with the deflection in *T. testis* consistently occurring distal of the sicular tip, a feature even more distinctly demonstrated in *T. cubitus* (Lenz and Kozłowska 2006); the thecal brim distal of the spines is smoothly rounded in *C. veles*, whereas *T. testis* often displays small-sized lappets immediately ventral of the spines (see Urbanek and Teller 1974; Lenz 1990; Lenz and Kozłowska 2006); and thecal spines of *C. veles* are directed slightly ventro-laterally, while those of *T. testis* are commonly directed dorso-laterally. The last feature explains why, in flattened specimens of *T. testis*, some of the spines are often seen to project from the dorsal side of the rhabdosome (see for example Urbanek and Teller 1974: pls. 22–24). In other aspects, such as strong and continuous ventral curvature of the rhabdosome, thecal profile, thecal symmetry, ovate outline of the thecal apertures, thecal spine development, and ventral curvature of the sicula, the two species are remarkably similar. Furthermore, development of the porus and its position very close to the aperture of the sicula is essentially identical; that in *Cochlograptus veles* is slightly closer to the sicula aperture (0.04–0.06 mm) compared with 0.06–0.08 mm in *Testograptus testis*, in either case corresponding to only two to four fusellar widths (Fig. 2A₂ versus 2E₂), although in some previously illustrated specimens of *T. testis* this distance may significantly exceed 0.1 mm (Lenz 1990). These differences are insignificant, however, when compared with the same feature in several species of other monograptids co-occurring with *C. veles*. For those, the gap ranges 0.25–0.38 mm, a greater than five-fold difference.

Phylogenetic relationships

There are two possible evolutionary modes to explain the close morphological parallelism between *Cochlograptus veles* and *Testograptus testis*.

(1) The two species represent parts of single lineage, in which their distinctive, shared characters originated once, presumably in early or mid-Telychian time with the origin of *C. veles*, and survived with some changes in rhabdosomal dimensions and shape through to the end of the early Homerian. If this hypothesis is correct and these two species represent part of a single, continuous lineage, then they should be placed within the same genus. In this case *Testograptus* should be regarded as the senior, subjective synonym.

(2) The second hypothesis is that the two species arose independently from some more or less straight, but different, monograptid with hooked thecae similar in broad characteristics to those of *Monograptus priodon*, and that the unique morphological similarity between the two species is the product of convergent evolution.

In consideration of the subtle, but very distinct morphological differences between the two species, noted above, our view is that the hypothesis of convergent evolutionary origin of

these two species is better supported by the available data than the single-lineage hypothesis. This view is further strengthened by two other factors: (i) the biostratigraphic gap between the last known occurrence of *C. veles* in the *Oktavites spiralis* Biozone and the occurrence of *T. testis* in the *Cyrtograptus lundgreni* Biozone, a gap of approximately 6–7 Ma and up to eight graptolite biozones (Melchin et al. 2004) in which no specimens remotely resembling either of these species has been discovered, and (ii) this interval includes an event of significantly elevated rates of graptolite extinction, the early Wenlock global Ireviken Event (see Melchin et al. 1998).

A cladistic analysis was undertaken in order to test our hypothesis that these two taxa arose independently. Nine taxa were compared: the two species under consideration, *C. veles* and *T. testis*, in addition to *Stimulograptus sedgwickii*, *St. utilis*, *St. halli*, *Monograptus marri*, *M. priodon*, *M. flemingii*, and *M.? cf. ayagusensis* Obut and Sobolevskaya (illustrated by Melchin 1987). The particular species of *Stimulograptus* and *Monograptus*, in spite of having more or less straight rhabdosomes, were selected because their thecal characteristics bracketed those of *C. veles* and *T. testis* respectively (see Fig. 5; also Loydell 1993; Loydell and Nestor 2006), and it was assumed that the ancestral species of both would almost certainly have been more-or-less straight. More significantly, it appeared to us that the thecal characteristics (e.g., amount of hook, shape of distal end of the meta-theca, overlap, inclination of interthecal septum) of *C. veles* were similar to those of *Stimulograptus* and particularly *Monograptus? cf. ayagusensis*, whereas those of *T. testis* were very like those in *Monograptus* (sensu stricto). The thecae of *M.? cf. ayagusensis* appear to be transitional in form between those typical of *Stimulograptus* and *Monograptus*. A further consideration was selecting taxa that were more or less within the biostratigraphic ranges of *Cochlograptus veles* and *Testograptus testis*, i.e., latest Aeronian/earliest Telychian to mid-Wenlock. In particular, *Stimulograptus sedgwickii* occurs in latest Aeronian while the other species of the same genus occur in lower to middle Telychian. *Monograptus? cf. ayagusensis* was reported by Melchin (1989) to occur in the *Monograptus crispus* and lower *Monoclimacis griestoniensis* biozones of the mid-Telychian.

Cladistic parsimony analysis (unweighted and unordered) was carried out using PAUP 4.0 (Swofford 2002) and MacClade 4 (Maddison and Maddison 2001), using *Stimulograptus sedgwickii* as outgroup. The Strict Consensus tree of four equally parsimonious trees is illustrated in Fig. 6. Tree length is 26, consistency index is 0.85, homoplasy index is 0.15, retention index is 0.82, and rescaled consistency index is 0.69. The results fairly clearly show *C. veles* on one subclade, while a second subclade holds *T. testis*, and that some species such as *M.? cf. ayagusensis* or closely related species of *Stimulograptus* (it is not clear whether *M.? cf. ayagusensis* is, in fact, assignable to *Monograptus* or *Stimulograptus*) is ancestral to *C. veles*. On the other hand, *M. flemingii* or some closely related species is more likely to be ancestral to *T. testis*. It appears then, that *C. veles* and *T. testis*

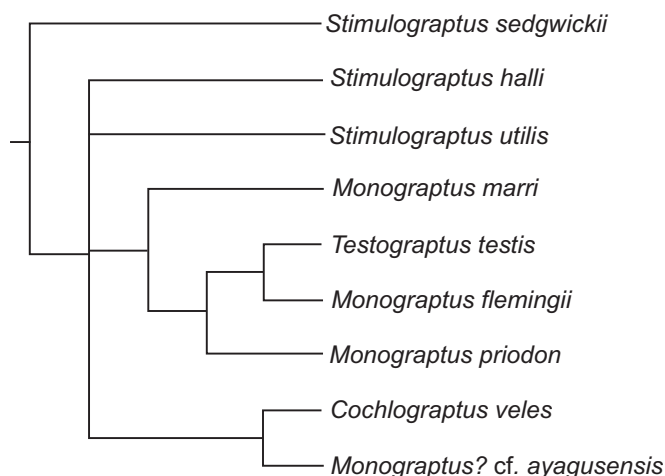


Fig. 6. Cladogram of nine species; *Stimulograptus sedgwickii* used as the outgroup. Bootstrap analysis shows that all dichotomous branches have 80% or greater bootstrap support except the *Monograptus flemingii*–*Testograptus testis* subclade, which is 74%.

were independently derived, and their remarkable parallelism is a product of convergent evolution.

Elles and Wood (1913: 423) noted strong similarities in thecal form between *Monograptus discus* (= *C. veles*) and *Cultellograptus cultellus*. Loydell and Nestor (2006) showed, however, that *Cultellograptus cultellus* possesses fully isolate, non-spinose, triangulate thecae, with strongly hooked apertures that point proximodorsally throughout.

If, as suggested herein, *C. veles* and *T. testis* are separate descendants from a *Monograptus* stem lineage, or independently derived from distinct monograptid genera (*Stimulograptus* versus *Monograptus*) then a case can be made for retaining them each in the distinct genera, *Cochlograptus* and *Testograptus*, as has been the recent taxonomic practice. Another possibility is simply to include these ventrally planispirally coiled, hooked monograptids within *Monograptus*. Until, however, a complete revision of the phylogenetic relationships among all of the Monograptidae has been undertaken, we prefer to maintain these distinctive taxa in their separate genera.

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Appendix 1

List of characters and character states.

1. Sricula shape: 0, straight; 1, curved
2. Sricula length (median value): 0, long (>1.4 mm); 1, 1.1–1.25 mm; 2, short (<1.0 mm)
3. Sricula: 0, no rutellum; 1, rutellum
4. Proscicular tip: 0, generally preserved and straight; 1, \pm preserved, deflexed ventrally
5. Pseudovirgula: 0, no; 1, yes
6. Rhabdosome: 0, \pm straight; 1, \pm weakly ventrally curved; 2, strongly ventrally curved.
7. Abrupt local ventral flexure: 0, no; 1, yes
8. Region of ventral flexure: 0, none; 1, distal of the sicular tip; 2, at or about tip of sricula
9. Keel-like protuberance at flexure: 0, none; 1, yes
10. Thecal shape: 0, *priodon* type, directed proximally; 1, directed ventro-proximally, but maintaining width of metatheca; 2, more claw-like in profile; e.g., *M. flemingii*
11. Inclination of interthecal septum: 0, 70–80°; 1, 50–60°; 2, 35–50°
12. Lappet-like lip anterior of spine region: 0, yes; 1, no
13. Proportion of width occupied by metatheca distally: 0, 45–60%; 1, 30–40%; 2, 25–30%
14. Thecal spacing, distal 2TRD: 0, >1.5 mm; 1, <1.4 mm
15. Origin of theca 1: 0, >0.1 mm from sicular aperture; 1, <0.1 mm from sicular aperture
16. Relative rate of rhabdosomal widening distally: 0, slowly; 1, rapidly

Appendix 2

Matrix table showing character number and character state coding for 9 taxa and 16 characters.

Taxon \ character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>Stimulograptus sedgwickii</i>	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0
<i>Stimulograptus halli</i>	0	1	0	0	0	0 and 1	0	0	0	1	0	1	0	0	1	0
<i>Stimulograptus utilis</i>	0	1	0	0	0	1	0	0	0	1	0	1	0	0	0 and 1	0
<i>Monograptus marri</i>	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	0
<i>Testograptus testis</i>	1	0	0	0	1	2	1	1	1	2	2	0	2	0	0 and 1	1
<i>Cochlograptus veles</i>	1	2	1	1	1	2	1	2	0	1	1	1	0	1	1	0
<i>Monograptus flemingi</i>	0	0	0	0	0	0	0	0	0	2	2	0	2	0	0	1
<i>Monograptus priodon</i>	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	1
<i>Monograptus</i> cf. <i>ayagusensis</i>	0	1	1	0	0	0	0	0	0	1	1	1	0	1	1	0